

A new dartless species of *Cahuillus* (Pulmonata: Helminthoglyptidae) from the Mojave Desert, California with a reassignment of *Eremarionta rowelli unifasciata*

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Abstract. A new species of the helminthoglyptid genus *Cahuillus* Roth, 1996 from the Mojave Desert of southeastern California, is described as *Cahuillus fultoni* n.sp. It lacks the dart sac and associated mucus glands of the female system found in all other members of *Cahuillus* including *Eremarionta rowelli unifasciata* (Willett, 1930), which is herein reassigned to this genus and elevated to species status as *Cahuillus unifasciata*. Sequence comparisons support the new species as distinct from other available taxa, based on combined analysis of 16S and COI mitochondrial gene regions for *Cahuillus fultoni* and four of the nominal taxa of *Cahuillus* or *Eremarionta* Pilsbry, 1913 within the Mojave. Although a relevant species, *Cahuillus greggi* (Miller, 1981), remains unsampled, the estimated phylogeny supports a sister species relationship between *C. unifasciata* and *C. fultoni*.

Key words: epiphallus, verge, whorl, homoplastic, Mojave National Preserve

Land snails of the New World family Helminthoglyptidae Pilsbry, 1939 inhabit several western and southwestern U.S. and adjacent Mexican states (Miller and Naranjo-García 1991). They are notably abundant and speciose in California where they represent 46 percent of the terrestrial molluscan taxa (Roth 1996).

In addition to shell features, helminthoglyptids are typically identified, at least in part, on the basis of characters of their hermaphroditic reproductive systems. This includes the presence or absence and placement of an accessory structure known as the dart sac along with an associated pair of membranous mucus glands. The dart sac produces a calcareous dart that is shot explosively into its mating partner during courtship. It carries a chemical agent that appears to promote the survival and utilization of the shooter's sperm (Chase 2007). Interestingly, ten described groups (genera/subgenera) of helminthoglyptid snails are notable for lacking the dart sac (Roth 1996, p. 35). Members of these dartless groups are typically found in arid regions. Four are represented in the Mojave Desert of southeastern California: *Sonorelix* Berry, 1943, *Mohavelix* Berry, 1943, *Herpeteros* Berry, 1947 and *Eremariontoides* Miller, 1981.

Miller (1970, 1973, 1981) and Miller and Naranjo-García (1991) advocated that dartless species evolved recently (post-Pluvial) by secondary simplification as a result of rapid genetic drift (*i.e.*, saltational speciation by chromosomal rearrangement) in desert populations decimated by rapidly-increasing aridity. Noting the similarity of shell characters

between certain dart-bearing and dartless species, they suggested that these species (or species groups) evolved independently. Using phylogenetic methodology, Roth (1996) provided strong evidence supporting a homoplastic loss of the dart-sac, showing that the dartless condition originated at least six times [including genus *Sonorella* Pilsbry, 1900 and its allies (his clade *Sonorellomorpha*)]. Alternatively, Schileyko (1991) advocated a monophyletic origin of the dartless groups and placed all dartless species in subfamily *Sonorellinae* Pilsbry, 1939 (of family Xanthonychidae Strebler and Pfeiffer, 1879). [Note: Bouchet and Rocroi (2005) place (a revised) *Sonorellinae* in family Helminthoglyptidae.] Anticipated molecular analyses should hopefully help support or refute contrasting hypotheses for the phylogenetic and biogeographic affinities of the treated genera (*e.g.*, Miller and Naranjo-García 1991, Cuzzo 1998) and better resolve the number of origins of the dartless condition.

The primary purpose of this paper is to report on an undescribed population of helminthoglyptid snails that exhibit the dartless condition. The reproductive anatomy of these snails is unlike that of all other dartless groups. This population is found in the Mojave National Preserve.

MATERIALS AND METHODS

Numerous snails were observed actively crawling on the surface during the late morning hours of 15 February

and on 14 December 2009 when specimens were hand-collected. Both occasions were sunny days following cold “winter” rainstorms.

For an investigation of the reproductive system, each snail was drowned overnight and removed from its shell on the following morning. Removal from the shell was initiated by immersion of the animal in 62 °C water for about 10 minutes. This causes protein breakdown in the body retractor muscle at its origin on the inner surface of the apex of the shell. Following immersion, the body was carefully pulled from the shell, breaking the muscle attachment. This procedure allows for both the shell and the soft anatomy to remain intact. The reproductive system was then dissected free from the other organs and removed. For clarity of internal structures and comparison with other specimens, each system was stained (Delafield Hematoxylin and Eosin Y) and slide-mounted with Permount (Gregg 1959, Naranjo-García 1989). Measurements of reproductive organs were taken from calibrated photographs of the entire freshly-dissected system prior to staining and mounting.

The scanning electron micrograph (SEM) of the embryonic whorls of the new species was taken at LACM with a Hitachi 3000N scanning electron microscope. The shell was cleaned and mounted on SEM stubs with clay and carbon-adhesive tabs and then sputter-coated with gold-palladium.

After the morphological and anatomical studies were completed, selected ethanol-preserved vouchers were sampled for DNA analysis by slicing a sliver of tissue from the side of the foot. DNA was prepared from this sample using a GeneJET Genomic DNA Purification Kit (Fermentas, Glen Burnie, Maryland) following the manufacturer’s included protocol. PCR and sequencing were carried out using standard DNA barcoding protocols at the Molecular Ecology Research Branch of the United States Environmental Protection Agency in Cincinnati, Ohio, using primers by HCO and LCO (Folmer *et al.* 1994) to amplify COI and the 16Sar and 16Sbr primers (Palumbi 1996) to amplify 16S.

Our combined data set has 14 newly-sequenced specimens representing six presumed species, and all of these new sequences have been deposited in GenBank (KC254695–KC254722) with voucher numbers and associated data. To root our tree, we also included a single distal outgroup voucher of a Mediterranean snail, *Xerocrassa mesostena* (Westerlund, 1879) (Helicoidea: Hygromiidae), whose 16S and COI sequences were downloaded from GenBank (JN701816 and FJ627058). Five specimens of the Big Sur shoulderband, *Helminthoglypta umbilicata* (Pilsbry, 1898), were sequenced for both 16S and COI and were used herein as a single functional outgroup. Quite a few sequences were available in GenBank from two fairly closely related genera, *Humboldtiana* Pilsbry, 1939 and *Sonorella*, but these were unfortunately available only for the 16S or the COI gene

region, respectively. We did not include these sequences in our presented combined gene analysis.

The multiple sequence alignment was performed with the online version 6 of the program, MAFFT (<http://mafft.cbrc.jp/alignment/server/>), with the Q-INS-i (with secondary structure of RNA considered) settings. Subsequent phylogenetic analysis was performed with PAUP* v. 4.0a125 (Swofford 2002) for parsimony and minimum evolution searches, and RaxML v. 7.2.8 (Stamatakis *et al.* 2008) for likelihood searches. Parsimony employed equal character weighting. Minimum evolution employed HKY85 distances. RaxML likelihood searches employed an online interface (<http://phylobench.vital-it.ch/raxml-bb/>) with a gamma model of rate heterogeneity, a mixed model with partitions corresponding to the separate genes and with proportion of invariant sites estimated from the combined data set.

Common names of snail species are from Turgeon *et al.* (1998). Abbreviations of institutions referred to in this article are: LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History; USNM, National Museum of Natural History; Smithsonian Institution.

Material examined.

LACM 1029, *Eremarionta rowelli amboiana* (Willett, 1931) (Type material: *Micrarionta hutsoni amboiana* Willett, 1931), holotype, 6 miles (9.7 km) NW of Amboy, San Bernardino County, California. LACM 177815, *Eremarionta rowelli amboiana*, rockslide in ravine about ¼ mile (0.4 km) east of Marble Mine (Iron Hat Mine), southwest side of Marble Mountains, San Bernardino County, California; 100+ shells. LACM 177816, *Eremariontoides argus* (Edson, 1912) (Type material: *Sonorella argus* Edson, 1912), south side of Holmwood Canyon, Argus Mountains, Inyo County, California, 3000 ft.; 63 shells. SBMNH 73270, *Eremariontoides argus*, Revenue Canyon, 1.0 mile (1.6 km) from rock crusher, in rockslides on north-facing slope, Argus Mountains, Inyo County; 12 shells. SBMNH 72933, *Eremarionta greggi* Miller, 1981, along road from Silver Lake to Camp Irwin, 11.4 miles (18.3 km) from Silver Lake, in rockslides just inside camp boundary, Avawatz Mountains, San Bernardino County, California, ca. 2,400 ft.; 32 shells. SBMNH 74611, *Eremarionta greggi*, south of Sheep Creek Spring, in rockslide, Avawatz Mountains, San Bernardino County, California; 30 shells. LACM 1023, *Eremarionta rowelli unifasciata* (Willett, 1930) (Type material: *Micrarionta hutsoni unifasciata* Willett, 1930), holotype, Newberry Springs, north end of the Kane (Newberry) Mountains, San Bernardino County, California. LACM 1024, *Micrarionta hutsoni hilli* Willett, 1930 (Jr. synonym of *Eremarionta rowelli unifasciata*, holotype, Sheep Hole Mountains, San Bernardino County, California.

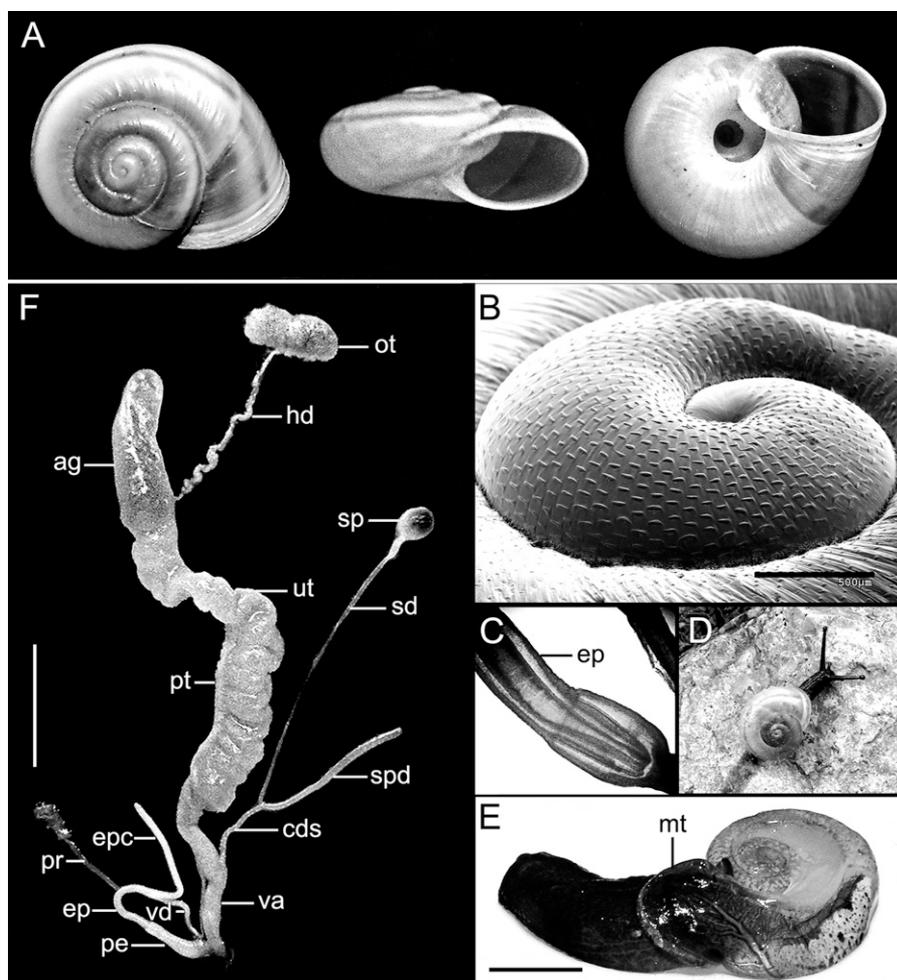


Figure 1. *Cahuillus fultoni* new species (clockwise from upper-left): **A**, Holotype, LACM 3215, apical, apertural and umbilical views; shell 12.2 x 6.0 mm; **B**, Paratype, LACM 3216, SEM of embryonic whorls, scale bar = 500 μ m; **C**, Paratype (snail #7), LACM 3216, distal, double-tubed epiphallus and penial sac with verge (slide-mounted specimen) horizontal field view about 1.2 mm; **D**, Live snail showing cryptic coloration, horizontal field view about 35 mm; **E**, Paratype (snail #7), LACM 3216, soft morphology showing extent of black pigmentation, scale bar = 5 mm; **F**, Paratype (snail #4), LACM 3216, hermaphroditic reproductive system (fresh dissection), scale bar = 5 mm. Abbreviations: **ag**, albumen gland; **cds**, common duct of the spermatheca; **ep**, epiphallus; **epc**, epiphallic cecum; **hd**, hermaphroditic duct; **mt**, mantle; **ot**, ovotestis; **pe**, penis; **pr**, penial retractor muscle; **pt**, prostate gland; **sd**, spermathecal duct; **sp**, spermatheca; **spd**, spermathecal diverticulum; **ut**, uterus; **va**, vagina; **vd**, vas deferens.

SYSTEMATICS

Helicoidea sensu lato

Family HELMINTHOGLYPTIDAE Pilsbry, 1939

Subfamily Helminthoglyptinae Pilsbry, 1939

Genus *Cahuillus* Roth, 1996 [Type species: *Sonorella wolcottiana* (Bartsch, 1903)]

Cahuillus fultoni Gilbertson, Eernisse, and Wallace, new species

(Figs. 1A–F, 2, 3; Tables 1, 2)

Diagnosis: Shell small for genus. Dart sac and mucus glands lacking.

Description of shell: (Figs. 1A–B; Table 1) Description based on holotype and nine paratypes (all fresh specimens). Shell small for genus (11.1 x 5.4 to 12.2 x 6.0 mm), depressed-globose, shiny, thin, semi-transparent, ranging from light brown to ivory-white in color with a brown to light tan shoulder-band bordered by lighter, whitish bands on last 1.2–1.5 whorls (showing on brownish shells). Whorls 4.0–4.3 in number. Embryonic whorls usually somewhat elevated, rounded, inflated, 1.5 in number on holotype, ornamented with discrete, regularly spaced, spirally arranged, elongated papillae. Neanic whorls rounded, with numerous, faint, radial growth striae. Body whorl becoming enlarged, rounded, last fourth whorl decurving to aperture. Aperture oblique, slightly wider than high, margins converging; peristome simple except along columellar margin where it is expanded. Parietal callus thin. Umbilicus moderately wide (mean = 0.21 times shell width; $N = 10$).

Description of body coloration:

(Figs. 1D–E) Entire dorsal body integument (including antennae) dark black. Melanin continuing onto mantle with lighter amounts on pallial membrane, outlining pallial vein; metanephridium (kidney) partly covered with black spots. Melanistic pigment shows through semi-transparent shell imparting a blue-gray coloration to most, or all, of body whorl (appearing cryptic on limestone rocks in its habitat). Mantle collar medium gray. Sole of foot gray with black borders.

Reproductive anatomy: (Figs. 1C, 1F; Table 2) Description based on 10 specimens. Hermaphroditic system with ovotestis embedded in liver as usual; hermaphroditic duct becomes undulated distally near albumen gland. Albumen gland and uterus typical in size and appearance. Free oviduct approximately as long as vagina, often entering vagina obliquely. Vagina of normal size and shape; dart sac and mucus glands lacking. Spermathecal duct with short, slightly inflated

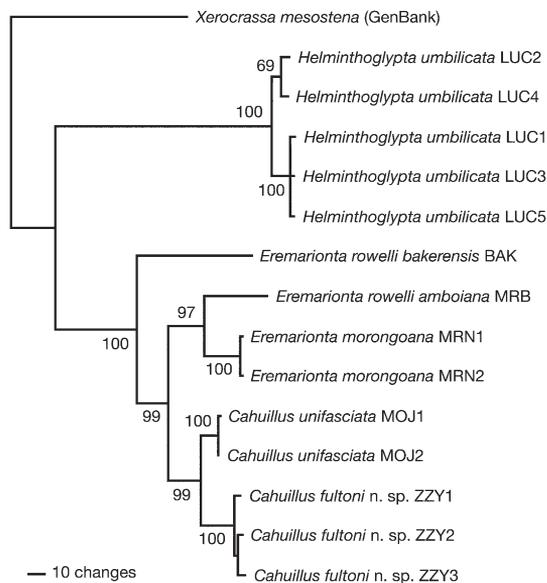


Figure 2. Phylogram of selected helminthoglyptid land snails including *Cahuillus fultoni* n.sp. Branch length is proportional to changes in a parsimony context. This tree depicts one of the three most parsimonious results ($L = 613$) of a combined 16S + COI data set. The other two most parsimonious trees differ only in the relationships among the outgroup, *Helminthoglypta umbilicata*. Bootstrap values have been added from separate 1000 replicate searches of this same data set. Voucher abbreviations (see text for more details): **LUC**, Landels-Hill Big Creek Reserve, near Lucia, Monterey County, CA; **BAK**, near Baker, San Bernardino County, CA; **MRB**, Marble Mountains, San Bernardino County, CA; **MRN**, Dry Morongo Canyon, Riverside County, CA; **MOJ**, Newberry Springs, San Bernardino County, CA; **ZZY**, Zzyzx Road off Interstate 15, Mojave Desert, near Desert Studies Center. The genomic DNA vouchers for this study, in order listed by locality, are as follows (also referred to as “CSUF DNA” numbers in the GenBank records, from the lab of DJE): LUC1-5: DE3420-24; BAK: DE2958; MRB: DE2949; MRN1-2: DE2961-62; MOJ1-2: DE2959-60; ZZY1-3: DE2951-52, DE2954.

diverticulum (about 0.4 times length of duct past junction with short common duct); portion of duct continuing to spermatheca moderate in length, very slender; spermatheca round, average in size, usually containing red material. Male system with prostate gland imbedded in uterus as usual; vas deferens relatively short and slender, proceeding alongside vagina to junction with penis, then continuing distally along penis to junction with epiphallus. Epiphallus about 1.5–2.0 times diameter of vas deferens, double-walled distally with internal lining of inner wall forming numerous minute folds projecting into lumen. Epiphallus inserts into penis apically with slender crease at junction. Epiphallic cecum present, moderate in length, bluntly-rounded (not tapering). Penial retractor muscle long, slender (contracted somewhat

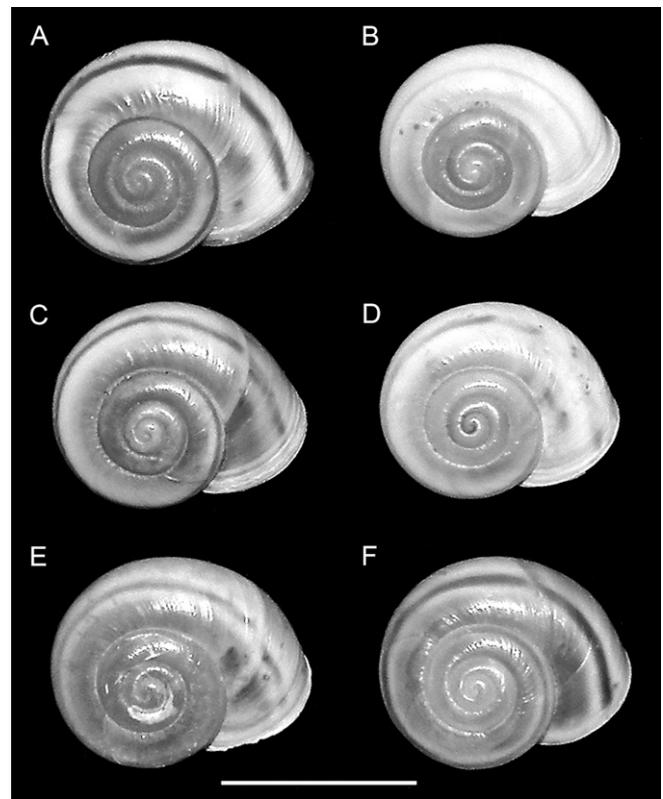


Figure 3. Apical view of selected Mojave Desert helminthoglyptid shells. **A**, *Cahuillus unifasciata* (*Eremarionta rowelli unifasciata*), LACM 177813; **B**, *Eremarionta rowelli amboiana*, LACM 177814; **C**, *Cahuillus fultoni* n. sp., holotype (brownish morph), LACM 3215; **D**, *Cahuillus fultoni* n. sp., paratype (whitish morph), LACM 3216; **E**, *Eremarionta (Eremariontoides) argus*, SBMNH 72933; **F**, *Cahuillus greggi* (formerly *Eremarionta greggi*), SBMNH 72933. Scale bar = 10 mm.

in illustrated specimen), with origin on lining of lung and insertion on epiphallus at about mid-length. Penis elongate, tubular, containing about 4–5 internal, longitudinal folds, slightly swollen apically enclosing a short, bluntly-rounded to elongate-conic verge with lumen of double tube of distal epiphallus continuing to apex of verge. Penis becomes more slender through mid-portion, then gradually expands somewhat distally before joining with vagina to form genital atrium.

Molecular analyses: Our results (Fig. 2), based on a combined 16S + COI data set for a modest selection of vouchers, are unambiguous in supporting each of the five presumed ingroup species as distinct, and assigned, based on reproductive traits, to either *Cahuillus* or *Eremarionta* Pilsbry, 1913. We also included a newly-sequenced species belonging to *Helminthoglypta* (s.s.) Pilsbry, 1939. Like our ingroup, this subgenus belongs

Table 1. Shell measurements (mm) of *Cahuillus fultoni* n. sp. Abbreviations: Dm = diameter, Ht = height, #Wh = number of whorls, ApW = aperture width, ApH = aperture height, UmW = umbilical width.

Shell	Dm	Ht	#Wh	ApW	ApH	UmW
1	12.0	5.5	4.1	7.0	5.6	2.4
2	12.3	6.4	4.1	6.5	5.5	2.1
3	12.2	5.4	4.3	6.7	5.5	2.6
4	11.4	5.8	4.1	6.5	5.5	2.5
5	11.7	5.7	4.2	6.5	5.3	2.9
6*	12.2	6.0	4.2	6.7	5.5	2.7
7	11.6	5.6	4.3	6.6	5.2	2.5
8	11.6	5.6	4.0	6.5	5.2	2.5
9	11.1	na	na	6.3	5.1	2.2
10	11.1	5.4	4.2	6.5	5.0	2.2
mean	11.7	5.7	4.2	6.6	5.3	2.5

* = Holotype

na = not available, shell partially broken

to the Helminthoglyptinae but its members are mostly from mesic coastal and mountain regions of California.

Parsimony analysis produced three minimum length trees of 613 steps, with a total of 285 parsimony-informative characters, only one of which is depicted here (Fig. 2). These three trees differed topologically only in minor grouping differences within our *Helminthoglypta umbilicata* outgroup vouchers. Minimum evolution and likelihood searches each supported an identical ingroup topology to our best parsimony results, and each had similar high support values for

Table 2. Lengths (mm) of freshly-dissected reproductive organs of *Cahuillus fultoni* n. sp. (specimen numbers correspond to shell numbers in Table 1). Abbreviations: CDS = common duct of the spermatheca, EpC = epiphallallic cecum, Pe = penis, SD = spermathecal duct from junction with diverticulum (including spermatheca), Sp# = specimen number, SpD = spermathecal diverticulum, and Va = vagina.

Sp#	Pe	EpC	Va	CDS	SD	SpD
1	2.4	4.2	2.6	2.9	15.6	8.5
2	2.8	3.9	2.7	3.0	11.1	5.1
3	2.0	5.2	2.6	2.3	16.3	6.0
4*	2.8	5.5	3.0	3.0	14.0	6.5
5	2.9	4.5	3.0	4.1	19.8	6.5
6	na	5.0	na	3.0	19.9	9.0
7	2.0	3.1	3.0	3.9	12.9	4.5
8	2.2	3.4	2.5	2.8	14.5	5.8
9	2.0	3.2	2.5	3.1	11.5	3.0
10	2.5	4.3	2.6	2.0	15.1	6.8
mean	2.4	4.2	2.8	3.0	15.1	6.2

* = illustrated specimen

na = not available

the same ingroup nodes supported in our parsimony results (Fig. 2). Likewise, separate analyses of 16S and COI portions of the data set each produced a single ingroup topology identical to that of our combined result.

Type material: Holotype, LACM 3215, shell (#6), DE2951 (genomic DNA used for sequences KC254695 and KC254709 in GenBank), and slide of reproductive anatomy. Paratypes: LACM 3216, five shells (#s 3–5,7, and coated shell for SEM), four slides of reproductive anatomies; SBMNH 213529–213533, five shells (#s 1, 2, 8–10) and five slides of reproductive anatomies; USNM 1180546, 9 shells. All specimens, Department of Interior, National Park Service MOJA-154.

Other voucher specimens: *Cahuillus unifasciata* (Willett, 1930) (= *Eremarionta rowelli unifasciata*), topotypes, LACM 177813, one shell, one slide of reproductive anatomy; SBMNH 213535, one shell, one slide. *Eremarionta rowelli amboiana*, SW side of Marble Mountains, in ravine about 0.5 km E of Marble Mine (Iron Hat Mine), San Bernardino County, California, 34.60°N, 115.53°W, 430 m AMSL, LACM 177814, one shell, one slide of reproductive anatomy; SBMNH 213534, one shell, one slide. For our molecular analyses, we included five vouchers of *Helminthoglypta umbilicata* (LACM 178544) collected from the University of California Landels-Hill Big Creek Reserve about 10 km NW of Lucia, Monterey County, California, 36.07°N, 121.60°W, 186 m AMSL (Above mean sea level).

Type locality: U.S.A., California, San Bernardino County, rocky slopes of southern Soda Mountains, immediately W of Zzyzx Road, about 0.5 km N of the Desert Studies Center (California State University System), 35.154°N; 116.106°W @ 285 m AMSL. Living specimens are known from hill slopes adjacent to the western shore of Pleistocene Lake Mojave (Soda “Dry” Lake) in Triassic metavolcanic rocks along with Permian limestone from localized outcrops. Bleached shells have been seen on higher slopes near the crest of this part of the Soda Mountains (crest = 661 m AMSL). The site is within the Mojave National Preserve.

On the lower slopes near the ancient lake shoreline the vegetation is dominated by Desert Holly (*Atriplex hymenelytra*), Allscale (*Atriplex polycarpa*), Alkali Goldenbush (*Isocoma academia ermophlia*) and Creosote Bush (*Larrea tridentata*) while on the higher slopes Creosote Bush and Brittlebush (*Encelia farinosa*) dominate.

The mean annual precipitation (in mm) at the nearby Desert Studies Center since 1986 is 93.2, and has ranged from 1.8 to 166.9. Live specimens are typically seen in years following significant winter rain events in late December, January or early February, particularly on days with high relative humidity or when the dew point has been hit during the morning hours. [Wiesenborn (2003) noted similar periods of activity for *Eremarionta immaculata* (Willett, 1937).] The temperature range (°C) since 1986 is from a high of 51.5 to a

Table 3. Shell diameter x height, and length measurements (mm) of selected reproductive organs of *Cahuillus unifasciata* (Willett, 1930) topotypes (Newberry Springs, California). Specimen 1, SBMNH 213535; Specimen 2, LACM 177813. Abbreviations: CDS = common duct of the spermatheca, EpC = epiphallic cecum, Pe = penis, SD = spermathecal duct from junction with diverticulum (including spermatheca), ShDxH = shell measurements (diameter x height), Sp# = specimen number, SpD = spermathecal diverticulum, and Va = vagina.

Sp#	ShDxH	Pe	EpC	Va	CDS	SD	SpD
1	13.4x7.7	2.3	4.1	4.0	2.9	15.4	7.5
2	12.8x6.9	3.5	5.0	3.1	3.0	13.0	6.0
mean	13.1x7.3	2.9	4.6	3.6	3.0	14.2	6.8

low of -13.3. Mean daily maximum/minimum temperatures for the months that the snail is active are: December 17/1, January 16/1, and February 21/4.

Etymology: The new species is named for Robert E. Fulton, site manager of the Desert Studies Center of the California State University System at Zzyzx. He discovered the snails in January 1993 and has assisted the authors as this project has progressed. Where a common name is useful, we propose “Fulton’s desertsnailed.”

DISCUSSION

In his monographic series on North American molluscs, Pilsbry (1939) listed *Micrarionta* Ancy, 1880 as one of three genera in his new subfamily Helminthoglyptinae. It included subgenus (formerly “section”) *Eremarionta* Pilsbry, 1913, whose type species, *Micrarionta desertorum* Pilsbry and Ferriss, 1908, has a type locality near Parker, Arizona. Pilsbry (1913: 382) remarked that his newly-proposed *Eremarionta* grouping “includes also *M. hutsoni* Clapp [= *Eremarionta rowelli hutsoni* (Clapp, 1907)] and probably also all the Californian and Lower Californian species which have been referred to *Sonorella*.” Berry (1943) erected the genus *Sonorelix* for species that were found to be dartless and whose embryonic whorls were “sculptured by a variably developed sub-retiform papillation.” Bequaert and Miller (1973) raised *Eremarionta* to full generic status based primarily on characters of the genitalia. Currently, this genus is restricted to about 18 species or subspecies found almost exclusively in the desert regions of southern California and western Arizona.

When Miller (1981) described *Eremarionta greggi*, from the rugged Panamint Range along the northern edge of the Mojave, he noted that there was a short inner tube within the outer tube of the distal epiphallus and that a short verge was formed by the partial eversion of this inner tube in the penial sac. Roth (1996) observed that this character was widespread

in the genus. He also noticed that some species originally listed by Pilsbry as “Group of *M. indioensis*” (Yates, 1890) from the Salton Sea region (region of the ancient Lake Cahuilla), plus *E. mexicana* Pilsbry and Lowe, 1934 and *E. greggi* showed a diagnostically different double-walled section of the epiphallus from the other species of *Eremarionta*. In these species, it is cylindrical (not conic) and < 0.4 times the length of the penis. Roth introduced the genus *Cahuillus* for their placement. The new species described herein shows this condition (length of double-tube = 0.20–0.41 times length of penis, mean = 0.30, $N = 8$) and is assigned to *Cahuillus* on this basis. Our molecular results (Fig. 2) imply *Cahuillus* might be nested within *Eremarionta* as presently construed; however, our molecular sampling of relevant species is too sparse to test the phylogenetic possibility of “*Eremarionta*” paraphyly, notably lacking DNA samples for the type species of these nominal taxa, and we have chosen to follow Roth’s (1996) anatomical diagnosis at present.

Cahuillus fultoni n. sp. shows strong affinities to *Cahuillus greggi* from the Panamint (T.L.) and the southern end of the Avawatz mountains, east of Ft. Irwin (Miller 1981) with regard to shell and genital characters (Figure 3F; Miller 1981). However, the shells of *C. greggi* are generally less depressed, have a more inflated body whorl, and exhibit a larger, rounder, more oblique aperture. With regard to reproductive anatomy, *C. greggi* is dart-bearing and shows some relatively minor additional differences such as a shorter double-tube of the epiphallus and a smaller verge.

The new species is also comparable to two of several subspecies of the widespread, dart-bearing eastern desertsnailed, *Eremarionta rowelli* (Newcomb, 1865) (Type locality: Tinajas Altas, in Tinajas Altas Mountains, Arizona). The shells of *Eremarionta rowelli unifasciata* are similar in most respects, including coloration, to the light-brown shells (the more numerous morph) of *Cahuillus fultoni* (Fig. 3C), but they are larger (holotype 13.5 x 6.1 mm) and exhibit a more prominent shoulderband (Fig. 3A). Their genitalia are also similar to those of *C. fultoni* including the presence of a double-tubed epiphallus continuing into the penial sac as a short, conic verge, diagnostic of genus *Cahuillus* (Fig. 4C). Hence, *E. r. unifasciata* is transferred to genus *Cahuillus* and raised to specific rank [= *C. unifasciata* (Willett, 1930)]. By comparison, shells referable to another subspecies, *Eremarionta rowelli amboiana* from the Marble Mountains are white (Fig. 3B) and, except for having a somewhat pale, more narrowed shoulderband, are nearly identical to the whitish shells (the less numerous morph) of *C. fultoni* (Fig. 3D). In addition, the mantle and the covering of the anterior visceral organs of *E. r. amboiana* are black, which imparts a bluish color to the body whorl of their semitransparent shells, similar to that of *C. fultoni*. This feature, along with their dark black body, makes living specimens of the two

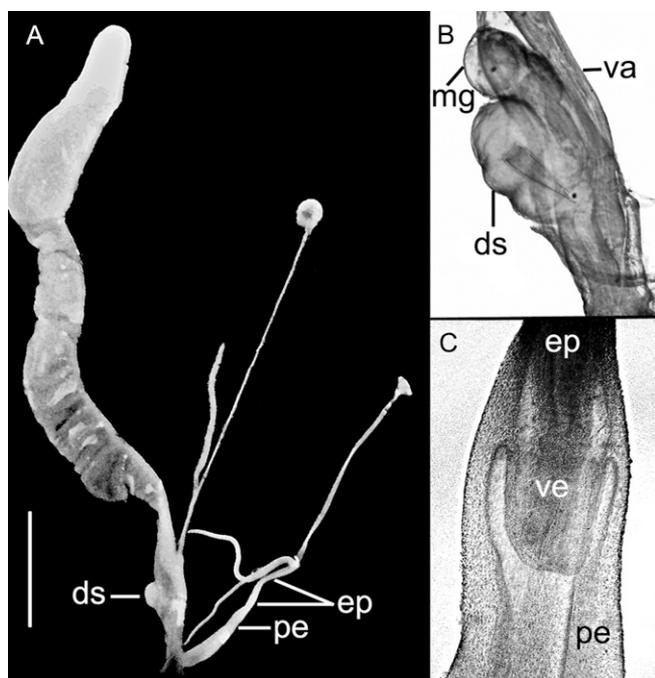


Figure 4. *Cahuillus unifasciata* (Willett, 1930). Topotypes. A and C, LACM 177813; B, SBMNH 213535. **A**, Reproductive system (fresh specimen), scale bar = 5 mm; **B**, Dart sac (containing dart) and bulb of mucus gland (stained, slide-mounted specimen), horizontal field view about 2.0 mm; **C**, distal epiphallus and proximal penis with verge (slide-mounted), horizontal field view about 0.6 mm. Abbreviations: **ds**, dart sac; **ep**, epiphallus; **mg**, bulb of mucus gland; **pe**, penis; **ve**, verge; **va**, vagina.

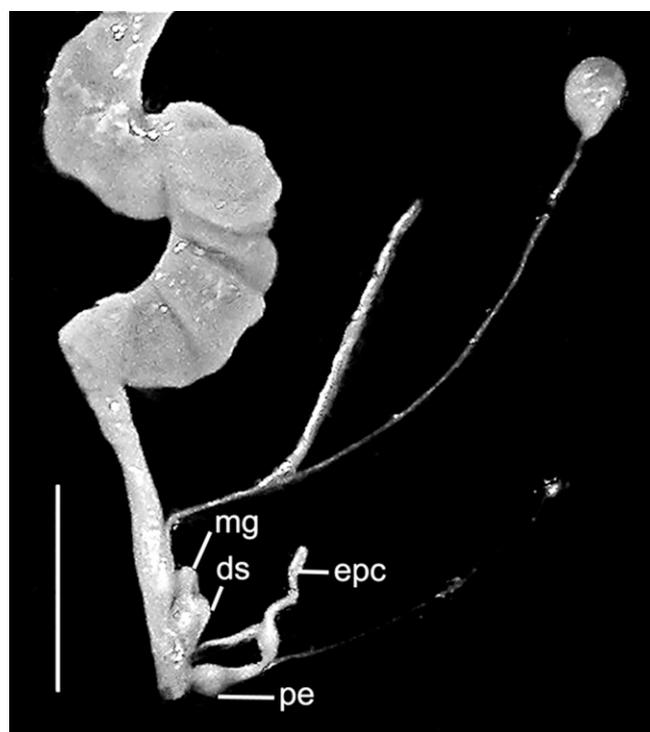


Figure 5. *Eremarionta rowelli amboiana* (Willett, 1931). LACM 177814. Reproductive system (fresh specimen) of a snail from the southwestern Marble Mountains, San Bernardino County, California. Abbreviations: **ds**, dart sac; **epc**, epiphallic cecum; **mg**, bulb of mucus gland; **pe**, penis. Scale bar = 5 mm.

species difficult to separate visually. However, their reproductive anatomies differ. In addition to possessing a dart sac and mucus glands, *E. r. amboiana* has much smaller, shorter male genitalia including a very short, inflated penis (ca. 1.0 mm in length) and a short epiphallic cecum (ca. 2.0 mm) (Fig. 5). Though smaller, the male organs are similar in shape, relative size and position to those of *E. r. hutsoni* (Clapp, 1907) (Pilsbry 1939, Fig. 115-2a).

Two dartless species, *Sonorelix avawatzica* (Berry, 1930) and *Eremarionta (Eremariontoides) argus* (Edson, 1912) (Fig. 3E) inhabit nearby mountainsides. However, both of these exhibit characteristic differences in certain aspects of their shells and genitalia compared to the new species and to each other (Berry 1943, Miller 1981).

Our molecular studies have provided results that are congruent with our anatomical separation of *Cahuillus fultoni* from other morphologically similar species of *Cahuillus* and *Eremarionta*. The results also support a predicted close relationship between *Cahuillus unifasciata* and the dartless *Cahuillus fultoni*, with the remaining caveat that the similar

Cahuillus greggi remains to be sampled. As discussed above, our molecular results resolve sampled members of *Eremarionta* as paraphyletic to *Cahuillus*, but the incomplete sampling of these genera and the lack of any nuclear gene markers sampled are reasons we hesitate to change the status of either genus based on these preliminary studies. In fact, these are the first sequences deposited in GenBank for any of about nine recognized species of *Cahuillus* and *Eremarionta*. Likewise, our new *Helminthoglypta umbilicata* sequences are the first mitochondrial sequences in GenBank for a genus of about 70 recognized species. These examples highlight the general lack of available sequence data for land snails from California, where these three genera are best represented.

It is evident that helminthoglyptid snails inhabiting the Mojave Desert are undergoing active speciation as various populations adapt to increasingly arid conditions. The loss of the dart sac and mucus glands appears to be a major component of their strategy for conserving water. In this regard, the new species lives in a particularly hot, arid, low-lying section of the Mojave. As currently diagnosed, based on reproductive characters,

Cahuillus is now understood to include the following species: *fultoni*, *greggi*, *indioensis*, *mexicana* and *unifasciata*. All of these species are dart-bearing except *fultoni*. *Cahuillus fultoni* is yet another species to join the increasing list of dartless taxa and our results support yet another independent origin of this condition.

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